Global Change Biology (2009), doi: 10.1111/j.1365-2486.2008.01812.x

Comparison of the impacts of consumers, ambient UV, and future UVB irradiance on mid-latitudinal macroepibenthic assemblages

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Abstract

Future levels in ultraviolet-B (UVB) radiation are expected to increase directly due to stratospheric ozone depletion and under water indirectly by, for example, global warming effects on DOC concentrations, altered trophic interactions in the plankton, or reduced eutrophication. While detrimental UV effects have been reported at the cellular level, little to nothing is known about community-wide effects of ambient and future UVB radiation. In a 4-month field experiment, the ambient UV regime was (i) reduced by cut-off filters which removed either UVB or total UV from the solar spectrum or (ii) increased to predicted future levels by UVB lamps. To allow relating the effects of present and future UV regimes to another important ecological control of community structure and diversity in subtidal marine habitats, consumer effects were quantified by an exclusion treatment under ambient light regimes. Ambient UV regimes did not affect community structure, biomass accrual, and diversity. In contrast, under enhanced UVB levels, the dominance of the competitively superior blue mussels increased and species richness and biomass accrual decreased. Species composition of the assemblages differed between the two UV regimes. Effects of enhanced UVB radiation and of consumption on biomass accrual, diversity, and structure of the community were comparable in magnitude and timing, but of opposite direction. In contrast, the effects of enhanced UVB radiation on growth and abundance of mussels were in the same direction, but shorter and weaker than consumer effects. Most UV effects were transitory and vanished within the first 2 months of succession. Our results indicate that present and future UVB levels may be of limited importance and not stronger in effect size than other ecological controls in structuring the shallow-water low-diversity macrobenthic communities in temperate regions.

Keywords: Baltic Sea, community structure, consumers, diversity, epibenthic assemblage, *Mytilus edulis*, seaweeds, species richness, succession, UV radiation

Received 8 July 2008 and accepted 20 October 2008

Introduction

Because of stratospheric ozone depletion, seasonal increases in ultraviolet-B (UVB) radiation have been reported from polar (Rex *et al*., 1997) as well as mid-latitudinal regions (Blumenthaler & Ambach, 1990). At the temperate region of both hemispheres, strong (up to 8%) anomalies in reduced total ozone concentration have been continuously reported over the last 20 years (WMO, 2003). In Europe, maximum values in ozone depletion have been recorded recently (Stick *et al*., 2005). Altered UV regimes are known to have detrimental effects on the physiology and ecology of photoautotroph and heterotroph organisms from terrestrial and aquatic habitats (Franklin & Forster, 1997; Caldwell *et al*., 2007). The expected recovery of the stratospheric ozone concentration to pre-1980 values over the next 50 years may implicate an amelioration of UVB effects for terrestrial ecosystems (WMO, 2003). However, there are

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at least three processes which, in benthic ecosystems, may counteract a decrease in atmospheric UVB during the second half of this century. First, evidence from long-term data suggest that the concentration of absorbing DOC in systems under strong riverine influence will decrease due to global warming (Schindler *et al*., 1996). Second, analysis of long-term data indicate that the transparency in coastal waters may seasonally increase as a result of global warming with zooplankton grazing under higher temperatures delaying phytoplankton spring blooms (Wiltshire *et al*., 2008) or as a result of mussel filtration (Mohlenberg *et al*., 2007). Third, a reduction of nutrient input in formerly strongly human affected systems such as the Baltic Sea could increase water transparency over the next decades (Wulff *et al*., 2007). Thus, aquatic organisms in coastal systems are likely to be affected by enhanced UVB hazards throughout the 21st century. Furthermore, because more animal species are sessile in aquatic than in terrestrial systems, behavioural avoidance of UV radiation may be less common under water than on land. This may further enhance the impact of UV radiation in aquatic ecosystems. Consequently, coastal epibenthic assemblages may be most vulnerable to UV effects, representing useful model systems to assess maximum UV effects at the level of communities.

The majority of UV studies tested physiological responses to UV exposure, such as changes in photosynthesis, often confirming detrimental effects on plants and algae across all life stages (Franklin & Forster, 1997; Caldwell *et al*., 1998; Roleda *et al*., 2007). Such physiological effects can modify species interactions and may thus reflect at the community level (Wahl, 2008a). For instance, UV-induced changes in secondary seaweed chemistry enhanced seaweed palatability and ultimately altered trophic interactions (Pavia *et al*., 1997). Similarly, but with opposite sign, freshwater diatoms were released from grazing pressure when UVB killed the consumers (Bothwell *et al*., 1994). When the impact of UVB differs among species, community function and composition will be altered by (i) selective mortality, (ii) shifting interactions, and (iii) differential growth rates. How environmental stress may be modulated ecologically has recently been described for an aquatic four-species interaction (Wahl, 2008b). Despite such possible profound ecological consequences, few experiments assessed UV effects at the level of communities. The limited available experimental evidence revealed inconsistent patterns. UV effects on the diversity of micro- as well as macrophytobenthic assemblages ranged from beneficial (Molis *et al*., 2003) via neutral (Hill *et al*., 1997) to detrimental (Dobretsov *et al*., 2005), or were of transient nature (Molis & Wahl, 2004). The latter suggests that assemblages can adapt to UV in analogy to protective mechanisms known at the cellular level (Franklin & Forster, 1997). For instance, if UV-resistant species proliferate and UV sensitive species are growth-inhibited under harmful radiation, the community may structurally rearrange until the former shade the latter (Karsten *et al*., 1998; Wahl *et al*., 2004). Interactions between other climate variables (e.g. salinity; Nygard & Ekelund, 2006), abiotic and biotic factors (Lotze & Worm, 2002), indirect effects across trophic levels (Bothwell *et al*., 1994), and differential susceptibility among life stages (Santas *et al*., 1998), render UV effects complex, nonlinear, and potentially strong enough to affect function and structure of communities.

Studies that combine climatic and ecological controls of benthic systems are extremely scarce (Lotze & Worm, 2002; Lotze *et al*., 2002; Zacher *et al*., 2007), though required, in order to compare the effect strengths of UV stress with better studied drivers of community dynamics. Particularly, field studies comparing the impact of ambient and predicted UV levels to other biotic drivers, for example grazing, are presently missing.

In this study we compare the impacts of the presumptive stressors ambient and future UVB irradiance to the impact of consumers on the diversity, species composition, and biomass accrual of a natural shallow-water macroepibenthic assemblage from a temperate region. Specifically, we asked (1) whether the impact of enhanced UVB radiation on the selected response variables was stronger than ambient UV effects, (2) how radiation and consumer effects compared with regard to the direction and magnitude of the impacts, and (3) whether the effects, if any, were transient or persisted at least to the end of the 4-month-long experiment.

Material and methods

Site description

A field experiment was conducted in a sheltered bay at Kiel Fjord, Germany (54°27′N, 10°09′E) between 12 June and 4 October 2001. Here, blue mussels (*Mytius edulis*) strongly dominate the low diversity shallow-water benthic community in abundance and biomass. The crab *Carcinus maenas* and the sea star *Asterias rubens* are the major benthic predators, mainly consuming *M. edulis*. The most abundant benthic grazers include the periwinkle *Littorina littorea*, the isopod *Idotea baltica*, and amphipods of the genus *Gammarus*. Schools of two-spot goby (*Coryphopterus flavescens*) and sticklebacks (*Gasterosteus aculeatus*) were seen in the bay, but no sign of fish predation was observed on the plots. Wave height at the sheltered study site was low (≤ 15 cm, M. Molis, personal observation) and the tidal range was ≤ 10 cm (personal communication, Water and

Shipping Bureau, Kiel, Germany). Mean salinity during the experiment was 16.4 (± 1.1 SD) at an average surface water temperature of 16.0 °C (± 1.8 SD, min. 14.5 °C and max. 18.3 °C).

Experimental design and set-up

The effects of radiation were tested under the following five radiation treatments ($n = 6$): (a) PAR + UVA + 2 × UVB: ambient irradiance enhanced with UVB lamps (313, Q-Panel, Cleveland, OH, USA) to twice the ambient intensity (hereafter PABB), (b) PAR + UVA + UVB: ambient irradiance after passage through a 3 mm Perspex filter (GS 2648; Röhm, Weiterstadt, Germany) (hereafter PAB), (c) PAR + UVA: ambient irradiance after passage through a 3 mm Perspex filter covered by 0.1 mm clear polyester copy paper (LTF NashuaCopy, Nashua, NH, USA) (hereafter PA), (d) PAR: ambient irradiance after passage through a 4 mm Makrolon filter (long life plus 293; Röhm) (hereafter P), (e) procedural controls: unfiltered ambient irradiance (Fig. 1 for spectral irradiance regimes). In addition, the effects of consumers at ambient irradiance levels (PAB) were manipulated, using open, partially open, and fully closed cages ($n = 6$). Partially open cages served as procedural controls.

A first set of blocks (filter-blocks) consisted of two moorings, each containing three matt-finished black Perspex rafts ($1000 \times 50 \times 5\,mm^3$) oriented in north-southerly direction. Spacing between moorings was 30m and 2.5 m between adjacent rafts within each mooring. In each raft (= block), five of six openings ($100 \times 100\,mm^2$) were covered with cut-off filters ($125 \times 125\,mm^2$). For constant emersion of filters, raft tops were lifted 1 cm above water level, using 20 mm thick Styrofoam sheets, glued with silicon to each rafts.

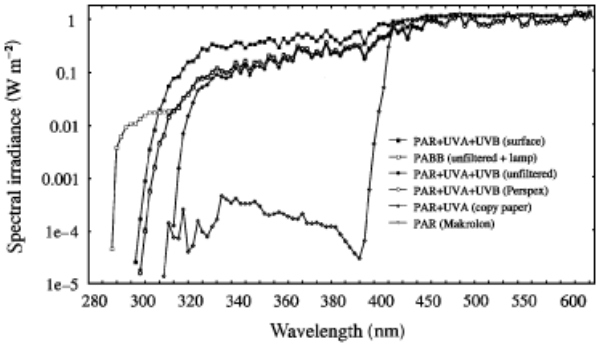

Fig. 1 Spectral irradiance (W m^{-2}) above the water surface, and at 0.04 m depth for the five radiation treatments. PAR, photosynthetic radiation (>400 nm); UVA, ultraviolet radiation (315–400 nm); UVB, ultraviolet-B radiation (<315 nm); PABB, ambient irradiance enhanced with cellulose diacetate filtered UVB lamp (>288 nm). Filter material given in parentheses.

Transparent polycarbonate containers ($100 \times 100 \times 100\,mm^3$) served as cages, into which ceramic tiles (= plots, $70 \times 70\,mm^2$) were fixed with Velcro in a horizontal position with their unglazed side facing upwards at a water depth of 40 mm. An $80 \times 80\,mm^2$ section was cut out of each container side wall. Afterwards a polyethylene mesh (1 mm^2 mesh size) was fixed to none, two, or four (= all) side walls to obtain open, partial, or complete cages, respectively. From a second set of blocks (lamp-blocks), three blocks were located alongside each of two wooden platforms ($10 \times 2.5 \times 0.6\,m^3$), moored ca. 5 m apart from and parallel to filter blocks. Each lamp-block consisted of one PABB plot and one unfiltered control plot and was separated by >2.5 m from adjacent lamp-blocks. Above each PABB plot, sealed UVB-transparent PVC pipes (1.5 m long, Ø 80 mm, GS 2648; Röhm) were mounted, containing one UVB-lamp (see Molis *et al*., 2003 for details). To avoid irradiation of control plots, UVB-opaque cardboard was wrapped around each lamp leaving only a $100 \times 100\,mm^2$ window that was placed 25 cm above each PABB plot. Cellulose diacetate foil was fixed over windows to block wavelengths <288 nm emitted by lamps (Fig. 1). Lamp emission in the UVA and PAR range was negligible (Fig. 1), reaching <1% beyond 360 nm compared with ambient irradiance levels (see Fig. 2 in Molis *et al*., 2003). Foils were replaced monthly to minimize transmission effects due to aging. As PABB plots, individual matt-finished black PVC rafts ($250 \times 250\,mm^2$) were either mounted with their central opening ($100 \times 100\,mm^2$) directly under each cardboard window (PABB) or 60 cm away (control), positioning ceramic tiles as described above. Functioning of lamps was ensured by a control wiring between lamps and a counter. Counter readings and position of windows were checked at least every second day and corrected when necessary. Counter readings did not differ significantly among plots during the experiment ($F_{5,559} = 0.632$, $P = 0.676$). Lamps were switched on daily between 9:30 and 17:30 hours by an electronic timer. Radiant energy of ambient PAR and UVA did not differ between plots from filter and lamp blocks (UVA: $F_{1,30} = 1.64$, $P = 0.210$ and PAR: $F_{1,30} = 1.29$, $P = 0.265$), indicating that different set-ups did not affect ambient irradiance regimes differentially.

Using a fine net (10 mm mesh size) that did not alter irradiance levels, we prevented birds to land on the plots. In addition, filters were cleaned every second day to minimize any reduction in transmittance as a result of, for example, salt spray.

Radiation measurements

For measuring spectral irradiance, we used a Bentham DM 150 double monochromator in Czerny-Turner arrangement (Bentham Instruments Ltd, UK). We

measured three wavebands within a 25 m range of all plots, using the RM-21 UV-meter and broadband sensors (Gröbel, Ettlingen, Germany) for UVB (280–315 nm), UVA (315–400 nm), and Vis-L (max. recording at 550 nm for measuring a PAR proxy in lux). Vis-L readings were converted into $W\,m^{-2}$ according to Lüning (1985).

Irradiance was measured above the water and for all three wavebands at 0.04 m (= depth 1), at 0.25 m for UVB only (= depth 2_{UVB}), and at 0.5 m for both, PAR and UVA (= depth $2_{PAR;UVA}$). Readings were taken simultaneously for all wavebands at each depth for 2 min, completing daily measurements of ambient irradiance within $\pm$ 15 min of local noon. Diffuse vertical attenuation coefficients of downward irradiance (K_d) were determined for each waveband from measurements at depths 1 and 2.

Assemblage sampling

Three randomly chosen subareas, that is 33% of total plot area, were nondestructively assessed on 10 and 24 July, 7 and 21 August, 11 September, and 4 October 2001 using a stereo microscope (12 $\times$ magnification). To avoid margin effects, subareas were not taken from a 1 cm buffer zone along the edge of tiles. Percent cover of each species was estimated in the subareas of each plot, from which mean species cover was calculated for each species. The Shannon-index was calculated from means of species abundance and species richness was recorded as the sum of species in the three subareas. Mussels were counted individually, grouped into five size classes, defined by the length of the longest axis of individuals and normalized to individuals cm^{-2}. Predetermined average biovolume per size class were used to calculate mussel growth as the difference in biovolume between sampling dates. As biomass parameters we measured wet (at every sampling) and dry mass. To measure wet mass, tiles rested 30 s vertically before weighing to the nearest 1 g. Because of massive growth, cover of the green alga *Ulva intestinalis* was trimmed after sampling to 1 cm above the holdfast whenever necessary, stored at $-20\,^{\circ}C$, and added to final biomass measurements. After the experiment, dry mass was determined by scraping all biomass off each tile, drying it at 60 °C to constant weight, and measuring it to the nearest 0.001 g.

Consumer abundance

Consumers were almost exclusively motile crustaceans, which stayed either cryptically in the mussel matrix of the species assemblage or escaped from our plots when tiles were taken out of the water for sampling. Consequently, only a coarse estimate of density was possible, preventing useful statistical analysis. Density typically ranged between 25 and 50 individuals cm^{-2}, with higher densities during the first half of the experiment.

Statistical analysis

To test for artefacts, Student's *t*-test compared (i) unfiltered and uncaged control assemblages from lamp- and filter-blocks to assess artefacts resulting from differences in block set-ups, (ii) unfiltered and PAB plots from filter blocks to assess filter artefacts, and (iii) open and partially caged PAB plots to assess cage artefacts. Before analysis of variance (ANOVA), we tested for homogeneity of variances (Cochran) and square-root transformed data where necessary. Data that were heteroscedastic after transformation were analysed by a Kruskal–Wallis test. Using repeated measures one-way ANOVAs, we examined radiation effects (four levels, fixed) over the complete duration of the experiment. We used mixed model two-way ANOVAs to test for effects of radiation (four levels, fixed) and block (six levels, random) at each sampling datum separately. We calculated sums of squares for blocks, but no variance ratios, that is 'block' was not treated as an experimental factor. Because of missing replication within blocks, no block $\times$ radiation interaction could be calculated. Sampling dates with significant filter or cage effects were discounted, but results presented for completeness. Where significant differences were found, Tukey honest significant difference test (HSD) tested for differences within groups. Adjusting *P*-values from multiple statistical tests by sequential Bonferroni correction was only done if the probability that tests were statistically significant due to chance alone was confirmed. To decide on this, the following formula by Moran (2003) was used:

$$P_{\mathrm{Moran}} = \left[\frac{N!}{(N-K)!K!}\right] \times \alpha^{K}(1-\alpha)^{N-k},$$

where N is number of tests (six in our study) and K is number of tests below α. A $P_{\mathrm{Moran}} < 0.05$ indicates that the probability of finding a significant test due to chance alone is very small and in this case, each significant ANOVA was accepted without Bonferroni correction.

To compare radiation and consumer effects, the log effect size was calculated for enhanced UVB, total UV, UVA, UVB, and consumer effects by division of measures from exposed plots and the respective control plots of the same block. For instance, the UVA effect size on wet mass was calculated as

$$\text{effect size} = \log(\text{wet mass PA} \times \text{wet mass } P^{-1}).$$

Direction and magnitude of radiation and consumer effects was graphically interpreted, where effects were

statistically significant if ± 95% confidence intervals did not overlap log effect size = 0.

The species composition of differently treated assemblages was compared with the nonparametric analysis of similarity (ANOSIM, Primer Software v5.0, Plymouth Marine Laboratory, Plymouth, UK), based on multispecies data. In case of significant ANOSIM results, we determined the relative contribution of species to dissimilarity, using SIMPER.

Results

Water transparency at the study site was consistently low (Table 1). At 0.04 m water depth, the irradiance level relative to surface irradiance was PAR = UVA = (1.49 × UVB), while at the greater water depth, the irradiance levels of UVA and UVB relative to surface irradiance was four times smaller than for PAR (Table 1). The coefficient of extinction increased with decreasing wavelength of the band considered. Temporal trends showed similar patterns for all three wavebands, with energy fluxes being June = July > August ≫ September. With increasing distance from the summer solstice, radiant energy decreased but this decrease was relatively stronger near the water surface (Table 1).

Altogether 10 macrobenthic species plus diatoms (as a grouped taxon) settled on the plots, including two species of green algae (*U. intestinalis*, *Ulothrix flacca*), two species of red algae (*Callithamnion corymbosum*, *Ceramium strictum*), one species of brown alga (*Pilayella littoralis*), and five species of invertebrates (*M. edulis*, *Balanus improvisus*, *Laomedea flexuosa*, *Clava multicornis*, *Polydora ciliata*). Three species, the red alga *C. corymbosum* and the hydroids *C. multicornis* and *L. flexuosa* never settled on PABB-exposed plots.

Under an ambient irradiance regime, assemblages were initially algal-dominated. During the first month of succession, total algal cover was 134 ± 36% (mean ± SD) with a relative share of 1 : 3 : 12 among *P. litoralis*, diatoms, and *U. intestinalis*, respectively, but decreased steadily to <10% in subsequent weeks. The opposite pattern was observed for blue mussels, which dominated the assemblage after the first 2 months of succession.

Biomass, diversity, and species composition

No significant block artefacts was detected for any of the response variables (all $t_{10} < 2.14$, $P > 0.058$, $R < 0.126$, $P > 0.089$). Significant cage artefacts were only detected for species richness and diversity (H') at the final sampling event (rest: $t_{10} < 2.12$, $P > 0.060$). Significant filter artefacts were only detected for species richness after 56 days.

Biomass. Only PABB and consumers impacted wet mass and this only in later successional stages (Fig. 2, Table 2) as indicated by a significant radiation × time interaction (Table 3). The probability of one test being statistically significant due to chance alone was negligible

Table 1 Mean (± SD) levels of ambient irradiance of three wavelengths (UVB, UVA, and PAR) above, 4 cm, and 25 (only UVB) or 50 cm (only UVA and PAR) below the water surface at the study site during the experiment

Time	Solar wave band	*n*	Radiant energy (W m^{-2})			K_d mean	% Surface irradiance at 0.04 m	% Surface irradiance at 0.5 (0.25) m
			Surface	0.04 m	0.5 or 0.25 m			
June–October	PAR	59	70.00 (± 39.9)	52.73 (± 26.93)	39.33 (± 21.02)	1.12 (± 0.58)	78.8 (± 14.9)	58.5 (± 11.1)
	UVA	59	32.82 (± 17.9)	22.26 (± 11.48)	4.51 (± 3.47)	3.77 (± 1.02)	73.0 (± 20.5)	14.5 (± 8.6)
	UVB	59	0.95 (± 0.41)	0.46 (± 0.22)	0.14 (± 0.08)	5.95 (± 1.34)	48.6 (± 9.2)	14.3 (± 4.5)
June	PAR	7	102.75 (± 8.47)	63.45 (± 13.73)	53.34 (± 11.05)	0.822 (± 0.65)	61.7 (± 11.9)	52.3 (± 13.1)
	UVA	7	42.32 (± 14.2)	21.57 (± 8.43)	4.95 (± 2.44)	3.34 (± 0.54)	51.9 (± 17.1)	11.5 (± 4.1)
	UVB	7	1.01 (± 0.29)	0.41 (± 0.13)	0.14 (± 0.03)	5.55 (± 0.48)	42.1 (± 9.5)	14.0 (± 1.9)
July	PAR	17	106.35 (± 45.6)	67.59 (± 10.15)	53.20 (± 22.28)	1.15 (± 0.39)	68.6 (± 17.9)	54.2 (± 15.5)
	UVA	17	44.10 (± 17.4)	27.94 (± 12.41)	5.63 (± 5.16)	4.01 (± 1.07)	64.6 (± 16.3)	12.1 (± 9.6)
	UVB	17	1.00 (± 0.39)	0.50 (± 0.22)	0.14 (± 0.08)	6.07 (± 1.01)	49.7 (± 9.9)	14.2 (± 4.6)
August	PAR	18	74.73 (± 5.93)	67.17 (± 10.15)	46.68 (± 7.11)	1.63 (± 0.42)	89.6 (± 10.9)	62.3 (± 7.2)
	UVA	18	32.20 (± 16.6)	24.44 (± 11.25)	4.33 (± 2.42)	4.01 (± 1.09)	80.0 (± 15.3)	14.2 (± 7.7)
	UV	18	0.79 (± 0.34)	0.44 (± 0.15)	0.13 (± 0.03)	6.08 (± 0.54)	58.4 (± 8.5)	14.8 (± 3.2)
September (and 2 October readings)	PAR	17	30.00 (± 22.5)	26.38 (± 19.87)	18.06 (± 15.40)	0.67 (± 0.42)	80.3 (± 6.5)	59.6 (± 10.2)
	UVA	17	18.27 (± 9.71)	14.91 (± 7.84)	3.39 (± 2.42)	3.46 (± 0.98)	82.6 (± 21.9)	18.5 (± 9.0)
	UVB	17	0.50 (± 0.20)	0.30 (± 0.11)	0.12 (± 0.03)	5.76 (± 0.51)	59.8 (± 12.3)	16.7 (± 3.7)

Vertical attenuation coefficient (K_d) and relative change of above surface irradiance at different depths indicate water transparency and surface reflection of ambient irradiance at each of the three wavelengths, respectively. *n* is number of daily measurements.

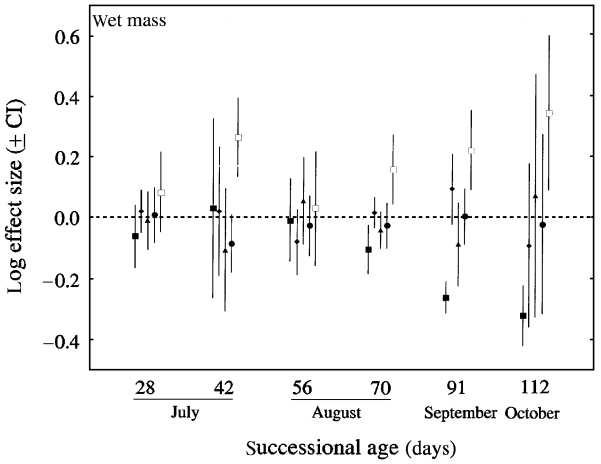

Fig. 2 Mean log effect size (± 95% confidence interval) of radiation and consumer treatments on wet mass of the macrobenthic assemblage at different successional age. Effect size was calculated as the ratio of wet mass (WM) on a given treatment and the WM on its respective control (see the following text) within a given block. Effect ratios of radiation treatments were all calculated with uncaged assemblages. The stippled line indicates no difference between control and differently exposed assemblages (ratio of 1). Treatments are significantly different where confidence intervals do not overlap with stippled line. Filled square, PABB effect (WM_{PABB}/WM_{PAB}); diamond, UVB effect (WM_{PAB}/WM_{PA}); triangle, UVA effect (WM_{PA}/WM_{P}); circle, total UV effect (WM_{PAB}/WM_{P}); open square, consumer effect ($WM_{PAB\text{-}o}/WM_{PAB\text{-}c}$). (Capitals in subscript are radiation regimes as in text, lower case letters in subscript are consumer treatments with c = caged and o = open.)

($P_{Moran} < 0.001$). PABB and consumers effects had almost the same temporal pattern, were of similar magnitude, but of opposite direction. Starting in late August (day 70), consumers increasingly enhanced, while PABB continuously suppressed biomass accrual relative to the controls significantly. At the end of the experiment, dry mass was significantly reduced up to 56% on PABB relative to PAB, PA, and P plots (ANOVA: $F_{3;20} = 11.25$, $P < 0.001$) and increased twofold on PAB panels exposed to consumers compared with caged PAB panels (Student's *t*-test: $t_{10} = 5.12$, $P < 0.001$).

Diversity (H′). PABB and consumers alone affected diversity, but significant effects were restricted to the early successional stage (Table 2), despite a just nonsignificant radiation × time interaction (Table 3). PABB significantly reduced average diversity relative to the other radiation treatments. Significant consumer and PABB treatments were at the same time effective, of comparable magnitude, but in opposite direction (Fig. 3, Table 4).

Species richness. PABB suppressed (relative to the other radiation treatments) and consumers stimulated species richness significantly at comparable magnitude, with all effects disappearing within the first 6 weeks of succession (Fig. 4, Table 2).

Community structure. Species composition was significantly affected by radiation treatments during the first 2 months of succession and by consumers throughout the entire study period (Fig. 5, Table 5). During the first month of succession, the species composition of PABB-exposed assemblages was significantly different to that of PAB-, PA-, and P-exposed assemblages (Table 5). During the remaining period when significant radiation effects were detected (i.e. the second month of succession until early August), PABB-exposed assemblages showed only a significant different species composition to PAB-exposed assemblages. Two taxa, *U. intestinalis* and diatoms, contributed strongest (up to 50%) and most frequently to the observed differences in species composition. PABB had detrimental effects on the abundance of *U. intestinalis* during the first 6 weeks of succession, but was of positive effect in early August (Table 5). Diatoms were always negatively affected by PABB, but this effect appeared to be significant only during the second month of succession (early July–early August).

Consumer effects on species composition were mainly due to changes in abundance of *P. littoralis*, *U. intestinalis*, and *M. edulis*, contributing together >60% to changes in assemblage structure (Table 5). Blue mussels (*M. edulis*) contributed strongest and most frequently to this difference, benefiting significantly almost throughout the experiment from the presence of consumers. In contrast, *P. littoralis* and *U. intestinalis* were both negatively affected by consumers, with significant contributions of *P. littoralis* occurring until late July, that is before the significant contribution by *U. intestinalis* was apparent (Table 5).

Mussel abundance and growth

Neither a significant filter nor block artefact was detected for data on mussel abundance and growth (all $t_{10} < 2.09$, $P > 0.064$). Significant cage artefacts were only detected for mussel abundance at one sampling datum (late August, day 70; rest: $t_{10} < 2.08$, $P > 0.064$).

Abundance. Only PABB and consumers had significant effects on mussel abundance. Significant PABB effects were only apparent during the first 6 weeks of succession (Fig. 6) as indicated by a significant interaction between radiation treatments and time (Table 3). The probability of one test being statistically significant due

Table 2 Results of mixed model two-way analysis of variance (ANOVA) or Kruskal–Wallis test (*P*-values in italics), if variances were heterogeneous after transformation, for separate sampling dates

		Wet mass			Diversity H'			Species richness		
	df	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
28 days (early July)										
Radiation	3	3.8	1.83	0.185	0.07	5.15	**0.012**	4.15	5.52	**0.045**
Block	5	8.6			0.01			0.84		
Residual	15	2.1			0.01			0.75		
42 days (late July)										
Radiation	3	54.2	0.65	0.594	0.17	17.32	<**0.001**	3.40	2.85	0.073
Block	5	135.0			0.01			2.10		
Residual	15	83.1			0.01			1.19		
56 days (early August)										
Radiation	3	64.3	0.78	0.525	0.14	3.50	**0.042**	4.15	3.32	**0.049***
Block	5	150.4			0.06			1.54		
Residual	15	82.8			0.04			1.25		
70 days (late August)										
Radiation	3	221.0	4.40	**0.021**	0.27	2.10	0.14	2.78	0.73	0.551
Block	5	205.1			0.05			3.17		
Residual	15	50.3			0.13			3.81		
91 days (September)										
Radiation	3	1723.4	16.27	<**0.001**	0.02	0.26	0.851	0.53	0.21	0.892
Block	5	91.8			0.30			5.96		
Residual	15	106.0			0.08			2.57		
112 days (October)										
Radiation	3		*13.19*	***0.004***	0.06	0.44	0.726	1.60	1.37	0.289
Block	5				0.03			0.94		
Residual	15				0.13			1.16		

		Mussel abundance (%)			Mussel growth		
	df	MS	*F*	*P*	MS	*F*	*P*
28 days (early July)							
Radiation	3	1068.6	6.26	**0.006**	0.00013	10.88	<**0.001**
Block	5	433.5			0.00030		
Residual	15	170.7			0.00001		
42 days (late July)							
Radiation	3	503.8	4.11	**0.026**	0.00013	0.72	0.554
Block	5	213.8			0.00015		
Residual	15	122.5			0.00018		
56 days (early August)							
Radiation	3	134.4	1.00	0.420	0.00203	0.87	0.478
Block	5	134.4			0.00660		
Residual	15	134.4			0.00233		
70 days (late August)							
Radiation	3	6.15	1.00	0.420	0.06782	11.79	<**0.001**
Block	5	18.5			0.00337		
Residual	15	6.15			0.00575		
91 days (September)							
Radiation	3	83.5	1.27	0.319	0.00681	1.75	0.200
Block	5	46.1			0.00327		
Residual	15	65.5			0.00390		
112 days (October)							
Radiation	3	19.1	1.00	0.420	0.00740	3.06	0.061
Block	5	19.1			0.00058		
Residual	15	19.1			0.00122		

Block was treated as a random factor for which sums of squares (MS) but no variance ratios were calculated. Because of missing within-block replicates, block × radiation interaction terms could not be calculated. Bonferroni-adjusted *P*-values are underlined. Significant differences in bold font; *filter artefact.

Table 3 Results of repeated-measures analysis of variances (ANOVAs) of radiation effects on various community response variables

		Wet mass			Diversity H'			Species richness		
Source	df	MS	F	P	MS	F	P	MS	F	P
Radiation (R)	3	5450.4	6.90	**0.002**	0.25	2.30	0.108	7.56	2.65	0.077
Residual	20	790.3			0.11			2.85		
Time (T)	5	45754.0	51.76	**<0.001**	3.97	66.28	**<0.001**	94.50	53.44	**<0.001**
T × R	15	2759.3	3.12	**<0.001**	0.10	1.74	0.056	1.81	1.02	0.439
Residual	100	884.0			0.06			1.77		

		Mussel abundance (%)			Mussel growth rate ($cm^3 day^{-1}$)		
Source	df	MS	F	P	MS	F	P
Radiation (R)	3	487.9	5.01	**0.009**	0.00996	57.28	**<0.001**
Residual	20	97.4			0.00017		
Time (T)	5	3216.4	31.68	**<0.001**	0.09960	37.24	**<0.001**
T × R	15	265.5	2.62	**0.002**	0.01414	5.29	**<0.001**
Residual	100	101.5			0.00267		

Significant results in bold font.

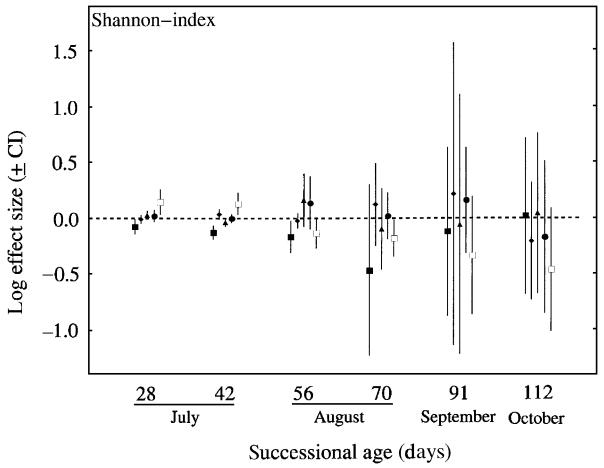

Fig. 3 Mean log effect size (± 95% confidence interval) of radiation and consumer treatments on Shannon-index of the macrobenthic assemblage at different successional age. Symbols and interpretation as in Fig. 2.

to chance alone was small ($P_{Moran} < 0.031$). Average mussel abundance was significantly enhanced in PABB treatments by up to 56%. In contrast to radiation effects, consumers significantly affected mussel abundance over almost the entire study period were of higher magnitude, albeit strongly decreasing in strength over time (Fig. 6). The direction of consumer and PABB effects was the same.

Growth. Only PABB and consumers significantly affected daily mussel growth rate and these effects were restricted to the early successional phase until early August, as indicated by a significant radiation × time interaction (Table 3). The probability of one test being statistically significant by chance alone was very small ($P_{Moran} < 0.030$). Significant effects of the presence of consumers and PABB occurred at the same time in succession were of the same (positive) direction but consumer effect was stronger than PABB effects (Fig. 7, Table 4).

Discussion

Simulated future UVB radiation provoked changes in the species composition and reduced both diversity and biomass accrual of the macrobenthic assemblage. Ambient UVA and UVB irradiance were not harmful. Consumers affected assemblages over comparable (diversity and biomass) or longer periods (species composition, growth, and abundance of mussels) and were of either opposite direction but comparable magnitude (biomass, diversity) or of comparable sign but stronger magnitude (growth and abundance of mussels) as compared with the effects of enhanced UVB radiation. Except for the impact on biomass, all effects vanished within several weeks.

Ambient UV was without effect on all tested uni- and multivariate responses of the epibenthic assemblages at the study site. This contrasts with findings from alpine freshwater and marine systems of the temperate region, where ambient UV levels detrimentally affected early successional stages of field grown epibenthic assemblages (e.g. Vinebrooke & Leavitt, 1999; Lotze *et al.*, 2002). Apparently, the species in the low diversity

Table 4 Mean (± SD) biomass, Shannon-index, species richness, mussel cover, and mussel growth rate for different radiation and consumer treatments at single sampling dates

Day	PABB	PAB	PA	*P*	No consumer (PAB)
Biomass					
28	10.40 ± 1.52	12.17 ± 2.64	11.50 ± 1.52	11.83 ± 1.94	10.00 ± 1.26
42	28.59 ± 16.22	23.23 ± 4.82	23.01 ± 9.18	28.04 ± 3.71	17.08 ± 7.84
56	36.07 ± 12.16	35.69 ± 7.70	42.79 ± 7.33	38.76 ± 11.74	36.82 ± 14.58
70	44.17 ± 12.38	55.00 ± 8.46	53.12 ± 8.13	58.38 ± 8.06	42.40 ± 5.50
91	42.20 ± 6.94	78.33 ± 8.89	64.67 ± 15.27	77.83 ± 7.68	48.33 ± 16.84
112	60.00 ± 7.65	135.0 ± 27.23	182.0 ± 85.90	159.7 ± 107.3	62.67 ± 20.26
Shannon-index					
28	1.09 ± 0.10	1.30 ± 0.09	1.32 ± 0.08	1.24 ± 0.14	0.95 ± 0.29
42	1.06 ± 0.12	1.41 ± 0.10	1.30 ± 0.06	1.42 ± 0.12	1.06 ± 0.17
56	0.82 ± 0.23	1.04 ± 0.17	1.09 ± 0.17	0.79 ± 0.26	1.41 ± 0.24
70	0.38 ± 0.39	0.85 ± 0.30	0.73 ± 0.38	0.80 ± 0.25	1.25 ± 0.22
91	0.46 ± 0.55	0.42 ± 0.32	0.29 ± 0.29	0.23 ± 0.20	0.78 ± 0.26
112	0.39 ± 0.37	0.28 ± 0.16	0.46 ± 0.28	0.50 ± 0.40	0.80 ± 0.42
Species richness					
28	6.33 ± 1.21	7.67 ± 0.82	8.00 ± 0.63	8.17 ± 0.75	5.17 ± 1.47
42	6.67 ± 1.51	8.33 ± 0.82	7.83 ± 1.47	8.17 ± 0.75	5.50 ± 1.87
56	5.33 ± 1.51	7.17 ± 0.75	6.17 ± 1.17	5.50 ± 1.05	7.83 ± 1.33
70	4.17 ± 2.56	5.33 ± 1.37	5.67 ± 1.37	5.50 ± 2.07	6.50 ± 0.84
91	3.33 ± 2.73	3.17 ± 1.47	3.50 ± 1.64	2.83 ± 1.17	5.67 ± 1.63
112	3.00 ± 1.26	2.83 ± 0.41	3.33 ± 1.21	4.00 ± 1.10	5.50 ± 1.52
Mussel abundance					
28	91.11 ± 14.40	58.33 ± 19.41	62.78 ± 14.82	69.72 ± 27.70	3.72 ± 4.05
42	98.89 ± 2.72	87.22 ± 11.04	80.56 ± 17.56	85.56 ± 13.77	5.78 ± 5.94
56	100.00 ± 0.00	88.33 ± 28.58	100.00 ± 0.00	100.00 ± 0.00	41.39 ± 30.01
70	100.00 ± 0.00	99.44 ± 1.36	100.00 ± 0.00	99.44 ± 1.36	47.56 ± 31.25
91	94.00 ± 12.00	100.00 ± 0.00	98.33 ± 4.08	100.00 ± 0.00	84.44 ± 15.15
112	100.00 ± 0.00	100.00 ± 0.00	100.00 ± 0.00	97.78 ± 5.44	83.33 ± 14.61
Daily mussel growth rate					
0–28	0.017 ± 0.01	0.007 ± 0.00	0.007 ± 0.00	0.008 ± 0.00	0.001 ± 0.00
29–42	0.020 ± 0.01	0.019 ± 0.01	0.013 ± 0.01	0.023 ± 0.01	0.004 ± 0.01
43–56	0.166 ± 0.07	0.126 ± 0.05	0.139 ± 0.06	0.159 ± 0.05	0.033 ± 0.02
57–70	−0.09 ± 0.1	−0.07 ± 0.05	0.128 ± 0.08	−0.09 ± 0.04	0.027 ± 0.02
71–91	−0.03 ± 0.04	0.016 ± 0.04	0.048 ± 0.10	0.000 ± 0.03	0.040 ± 0.01
92–112	0.006 ± 0.01	−0.01 ± 0.02	−0.05 ± 0.06	−0.02 ± 0.02	0.039 ± 0.01

assemblage at our study site are adapted to actual UV levels. This was not necessarily to be expected because recruits may stem from deeper and more UV-protected water depths. In contrast, negative effects were observed under an irradiance regime of simulated future UVB levels. Here, both species of hydroids and one red alga did not recruit and the abundance of the brown seaweed *P. littoralis* was reduced. Thus, about 40% of the encountered species at the study site were sensitive to and damaged by enhanced levels of UVB. Apparently, their local population does not contain genotypes preadapted to future UVB levels or capable to phenotypically adapt to them.

The absence of effects by ambient UVA or UVB is unexpected as such impacts on comparable communities have been described for temperate (Wahl *et al*., 2004) and polar regions (Zacher *et al*., 2007). In addition to season, weather, and latitude, water transparency strongly influences underwater UV levels (Jerlov, 1950). For instance, increased DOC concentration in the water can attenuate UV effects on diatom assemblages (Kelly *et al*., 2001). Our *in situ* measurements indicate that the water transparency at the study site was low for UVB during the experiment. Half of the ambient above surface UVB irradiance was already absorbed at 4 cm water depth where the experimental assemblages were positioned. If the Baltic Sea becomes more transparent to UVR in the future as a result of warming-mediated decreases in land-based DOC-input (yearly inflow of 479 km^3 of water from river drainage;

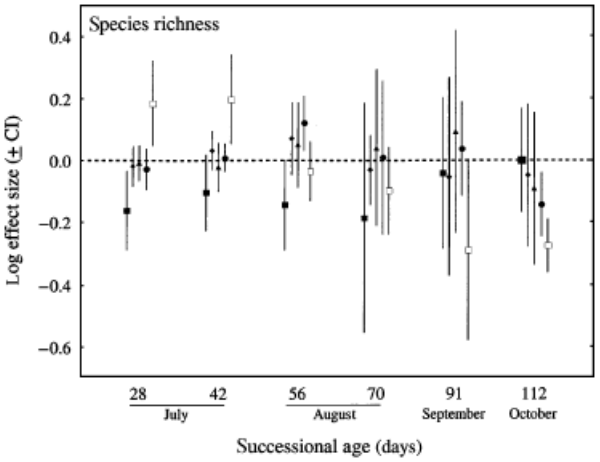

Fig. 4 Mean log effect size (± 95% confidence interval) of radiation and consumer treatments on species richness of the macrobenthic assemblage at different successional age. Symbols and interpretation as in Fig. 2.

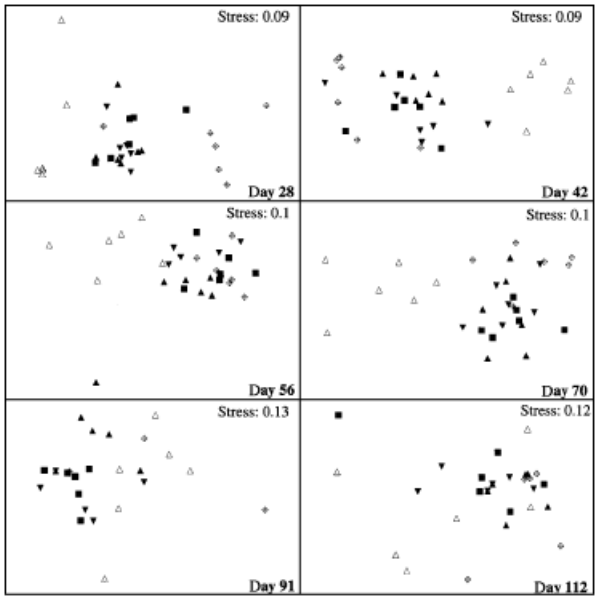

Fig. 5 Multidimensional scaling (MDS) plot on species composition of macrobenthic assemblages at different successional age. Filled symbols indicate treatments at ambient irradiance regimes with grazer access (triangle, PAB; inverted triangle, PA; square, P; open triangle, caged PAB; crossed diamond, PABB). Stress indicates level of agreement between Bray–Curtis coefficients of similarity and rank order of distances between and among groups in the MDS plot.

Dietrich & Schott, 1974), of decreasing levels of eutrophication, or of altered trophic interactions in the plankton, levels of damaging UVB irradiance for shallow water assemblages might increase and thus affect assemblages as indicated by our enhanced UVB treatment. Because this study shows that some local species cannot adapt to enhanced UVB within one generation, the effect of putatively increased UVB radiation in the future will depend on the rate of change in radiation. About 60% of the local species, on the other hand, were able to cope with enhanced UVB levels. A number of explanations seem possible. First, several species of seaweeds were shown to acclimate to UV conditions. For instance, the viability of kelp spores was dependent on the depth at which parental sporophytes occurred, suggesting preacclimatization (Wiencke *et al*., 2004). Second, some species of invertebrates, micro-, and macroalgae can protect themselves against UV by the use of UV-absorbing substances (Gleason & Wellington, 1995; Pavia *et al*., 1997; Karsten *et al*., 1998) and kelp species are known to light harden as they mature (Franklin & Forster, 1997). Finally, protective shading by UV-resistant species of the assemblage (e.g. *Ulva*) might have created UV-free microhabitats in which UV-sensitive species could successfully recruit, corroborating previous results from the same study site (Molis *et al*., 2003). The possibility of protective shading by UV-resistant species has also been reported to occur in other macrobenthic assemblages (Molis & Wahl, 2004) and microphytobenthic mats, where UV-resistant species constitute the top layer, providing a physical refuge for UV-sensitive species below (Karsten *et al*., 1998). A diatom film on the substratum may offer protection for UV-sensitive macrobenthic larvae and spores (Vinebrooke & Leavitt, 1999). Under enhanced UVB levels, protective shading may be jeopardized when 'umbrella' species are themselves affected, such as diatoms in this study.

In this study, consumer effects on biomass, species richness, and diversity were of opposite direction but similar in their magnitude and timing to the effects of enhanced UVB radiation. Consumers were mainly small crustaceans such as amphipods and isopods. These mesograzers have the potential to alter the structure of macrophytobenthic communities (e.g. Duffy & Hay, 2000). Because the effects of mesograzers were opposite in direction to the effects of enhanced UVB radiation, changing UVB regimes in the Baltic Sea have the potential to affect the structure of epibenthic communities differently than presently acting ecological factors. Interactive effects between consumers and UVB radiation have been reported, and trophic interactions altered by UV radiation (Pavia *et al*., 1997) may indirectly transfer radiation effects to the community level. Despite their general importance, however, UVB effects did not persist in the benthic communities investigated here. This was due to positive UVB effects on blue mussels (*M. edulis*). Their insensitivity to UV as compared with other components of the assemblage

Table 5 Global ANOSIM results (*R*, *P*) and significant pairwise comparisons for radiation and consumer effects on species composition of macrobenthic assemblages at different times during succession

	Filter artifact		Radiation effect					Cage artifact		Consumer effect	
	R	*P*	*R*	*P*	PAB vs. PABB (%)	PA vs. PABB (%)	P vs. PABB (%)	*R*	*P*	*R*	*P*
28 days	0.09	0.14	0.26	**<0.01**				−0.13	0.46	0.70	**<0.01**
			Pilayella littoralis		44 −	45 −	42 −			19% −	
			Ulva intestinalis		14 +	15 +	16 +			nc	
			Mytilus edulis		12 +	9 +	10 +			46% +	
42 days	0.25	0.052	0.26	**<0.01**				0.00	0.437	0.99	**<0.01**
			Diatoms		37 −					nc	
			Ulva intestinalis		17 +					nc	
			Mytilus edulis		nc					32% +	
			Pilayella littoralis		nc					22% −	
56 days	0.45	<0.01	0.13	**0.02**				−0.07	0.701	0.47	**<0.01**
			Diatoms		18 −					nc	
			Laomedea flexuaosa		18 −					nc	
			Ulva intestinalis		16 −					29% −	
			Mytilus edulis		nc					30% +	
70 days	−0.03	0.56	0.11	0.07				−0.01	0.751	0.79	**<0.01**
			Ulva intestinalis							35% −	
			Mytilus edulis							28% +	
91 days	0.08	0.22	0.01	0.38				−0.09	0.784	0.33	**0.022**
			Ceramium strictum							29% −	
			Diatoms							25% −	
			Balanus improvisus							20% −	
112 days	−0.04	0.65	0.00	0.45				0.17	0.121	0.27	**0.026**
			Polydora ciliata							35% −	
			Mytilus edulis							32% +	

SIMPER results on the relative contribution of single species on significant community composition responses to radiation and presence of consumers. +: positive and −: negative give the direction of effects for each species. nc: no contribution.

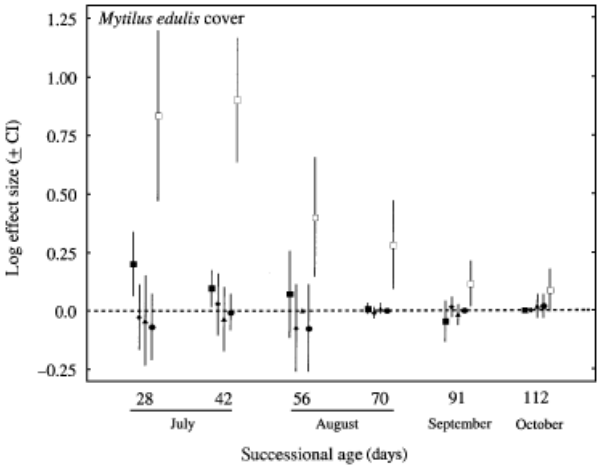

Fig. 6 Mean log effect size (± 95% confidence interval) of radiation and consumer treatments on mussel abundance at different successional age. The apparent discrepancy between log effect size and mean mussel abundance in Table 4 comes from use of arcsin-transformed and untransformed data, respectively. Symbols and their interpretation as in Fig. 2.

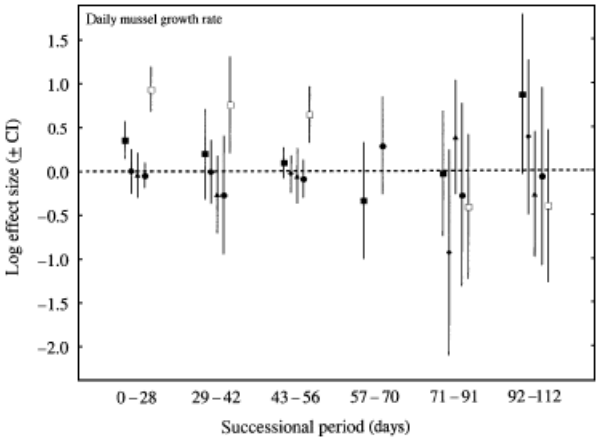

Fig. 7 Mean log effect size (± 95% confidence interval) of radiation and consumer treatments on daily mussel growth at different successional age. No effect ratios could be calculated for the period 57–70 days when PA treatments were used, due to positive growth rates under PA and negative growth rates under remaining radiation regimes. Symbols and their interpretation as in Fig. 2.

 Global Change Biology, doi: 10.1111/j.1365-2486.2008.01812.x

allowed mussels, as the competitively dominant species of the system (Dürr & Wahl, 2004), monopolizing the assemblages under enhanced UVB already after the first month of the experiment. A comparable level of mussel abundance under ambient light regimes took twice as long to establish. Once all substrata were mussel dominated, differences in species composition among radiation treatments disappeared. Because the presence of consumers was also beneficial for mussel growth and abundance, mussels were able to monopolize the assemblage fastest in assemblages exposed to both stressors, consumers, and UVB radiation.

Transitory UV effects seem to be common at the community level (Wahl *et al*., 2004). Early live stages often show highest UV sensitivity (Franklin & Forster, 1997; Roleda *et al*., 2007). Possibly the recruiting stages of the most sensitive species in this study (the red alga *C. corymbosum* and the hydroids *C. multicornis* and *L. flexuosa*) were killed when exposed to the enhanced UVB and the recruitment period was too early for UV-protected microhabitats to have established on the substratum. At the other end of the sensitivity gradient, mussels and the green alga *U. intestinalis* showed higher growth rates and recruitment success under the enhanced than under the ambient UVB regime, corroborating earlier findings (Molis *et al*., 2003) and, thus, indicating that similar community responses to enhanced UVB radiation occur in different years for the studied assemblage. This suggests that the observed differences in species composition are driven by very different, sometimes opposing species-specific, yet reproducible responses to UVB.

This experiment indicates that, despite detrimental effects on some species, a possible future increase of UVB levels does not necessarily reflect on the structure and diversity of a community. In such macrobenthic assemblages, where the dominating species is insensitive to or even benefits from UVB such as *M. edulis* in the Western Baltic (this study), present and future irradiation stress may be ecologically buffered. Such ecological buffering of ambient UV radiation by various UV-insensitive species has also been reported from tropical to subartic regions spanning nutrient-poor to upwelling systems for red algae (*Ceramium* spp.) in Australia, China, and Namibia, for green algae (*Ulva* spp.) in Australia, China, Chile, and Israel, and for brown algae (*Chordaria* spp.) in Canada (Wahl *et al*., 2004). This suggests that the limited UV effects that we reported here for a mid-latitudinal mussel-dominated assemblage may also apply in other regions. Similar experiments on different types of communities at sites of different ambient UV regimes could clarify this question.

Acknowledgements

We thank H. Sandmann for assistance in the field and calibration of UVB lamps. Technical support for UVB lamp calibration by the Bundesamt für Strahlenschutz is acknowledged. We are thankful for gratis supply of UVB lamps by Pausch Ldt. We are grateful to the staff of WSA Kiel for allowing setting up the experiment at the Schleuseninsel Holtenau. Technical support by workshop staff of the CAU Kiel is greatly acknowledged. Financial support was given by DFG fund WA-708/6-1 and 6-2 to M. W.

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 Global Change Biology, doi: 10.1111/j.1365-2486.2008.01812.x